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Figure 1. (Top) Black spruce boreal forest contains abundant bryophytes and lichens in the understory.

Figure 2. (Bottom) Some mosses are only found in wet fen margins.

Figure 3. (Left) *Sphagnum squarrosum*.

Photograph by Gary A. Laursen

Beneath My Feet: Alaska's Miniature Forests

By Rodney D. Seppelt and Gary A. Laursen

Abstract

Mosses are important components of low-lying vegetation of terrestrial ecosystems in most regions of the world, from the tropics to high altitude alpine and high latitude Arctic and Polar Regions. Throughout the boreal forest, alpine and Arctic tundra regions, both mosses and lichens may comprise a large part of the aboveground plant biomass. Extensive *Sphagnum* dominated peatlands in boreal regions are a well-known example of the potential, but the all too often unrecognized, dominance exhibited by mosses in various habitats. In Alaska there are at least 650 species of moss, 280 hepatics, but only one hornwort.

Introduction

Mosses, together with related groups, the liverworts and hornworts, collectively belong to a group of plants known as the Bryophytes. World wide there are a conservative 15,000 to perhaps an overestimate of 25,000 different species. They are typical green plants with chlorophyll a and b as their primary photosynthetic pigments, starch as an energy storage product, and may have been amongst the earliest of the land plants. They are known to date back

as far as 300 million years in the fossil record. Bryophytes are generally small because they lack functional vascular tissues for internal water conduction and support. Water and nutrient absorption is primarily over their surfaces. The largest truly terrestrial moss, *Dawsonia superba* of Australia, New Zealand and nearby islands, reaches up to 30 inches (75 cm) in height. In the northern hemisphere, some *Fontinalis* species growing on rocks in streams may be longer, but the shoots are supported by the water. The smallest mosses are less than 0.04 inch (1 mm) tall with most in the 0.4-2.4 inch (1-6 cm) range.

Bryophytes are significant components of the biodiversity found in many habitats such as tundra, boreal forest tree line (Figure 1), peatlands and wetlands (Figure 2). They are able to colonize hard substrates such as rock (Figure 4) and bark surfaces (even old cars and buildings), and are primary colonists of recently uncovered or disturbed soil surfaces (Figure 5) such as those exposed by glacial recession, land slips, and fire denuded surfaces. They play a major role in the stabilization of substrates preparatory to colonization by vascular plants (Figure 6). Many bryophytes have a high tolerance for long periods of desiccation, high and low temperature and extreme daily temperature ranges of 120° F (50° C) or more. In Japan, the liverwort *Jamesoniella vulcanicola* lives in volcanic fumarole streams in highly acidic water

with a pH range of 1.9-4.6 (Yokouchi *et al.* 1984). Apart from occupying a wide range of habitats, bryophytes provide specific substrates for many fungi (Figures 7, 8, 9), shelter for small mammals and a host of tiny invertebrate animals, a seed bed for higher plants, nest materials for birds and animals, and important ground cover insulation (Figure 10). They play a significant role in nutrient cycling, absorption of moisture, and in the carbon and nitrogen balance of high latitude ecosystems. Bryophytes and lichens are amongst the most sensitive indicators of atmospheric pollutants such as heavy metals, radioactive fallout, sulfur dioxide and nitrogen oxides as acid rain, and their effects on ecosystems of the world. They are also fascinating subjects of scientific study, aesthetically pleasing and beautiful (Figures 11, 12) but, sadly, all too often ignored.

In Alaska there are at least 650 species of moss, 280 hepatics and just one hornwort (W.B. Schofield, *unpublished lists*). In the genus *Sphagnum*, an important component of the moss flora of peatlands and wetlands, there are in Alaska 53 of the 97 species known from continental North America (McQueen and Andrus 2007).

The Life Cycle

Like vascular plants, the bryophyte life cycle (Figure 13) involves an alternation of two generations—a

gametophyte (bearing the male and female reproductive structures) and a sporophyte, a specialized structure formed after fertilization and bearing the tiny spores in a capsule at its tip (Figure 14). Unlike vascular plants, however, the dominant generation in bryophytes is the gametophyte plant. In mosses the gametophyte is a leafy structure. In liverworts it may be either leafy or thallose (flattened and ribbon like). In hornworts the gametophyte is thallose.

All bryophytes need free standing

water for growth and reproduction. Motile sperm from the male antheridium are released at maturity and swim in a film of water to a flask-shaped female archegonium, containing the egg cell. After fertilization the resulting zygote develops into a very different structure, the sporophyte, which has at its upper end a capsule that bears the spores. After being released, spores germinate usually via a filamentous or thread-like stage, on which will eventually develop new gametophyte plants. At the mouth of the

capsule of many mosses are specialized and architecturally beautiful structures called the peristome teeth (Figure 15) which help to control spore liberation. The peristome teeth spread when dry and close over the capsule mouth when moist, thereby regulating spore liberation.

Duration of the life cycle varies considerably. It may be as short as two weeks to as long as several years. In the thallose liverwort *Riccia cavernosa* (Figure 16) found growing on silt shelves and sand banks along Arctic rivers such as the

Kobuk, the life cycle is as short as two to three weeks. For the same species in temperate latitudes it is two to three months. Dung inhabiting mosses such as *Splachnum luteum* (Figures 17) and *Tetraplodon* (Figure 18), may take two to three years to produce mature sporophytes.

In addition to reproducing sexually, bryophytes produce a variety of specialized asexual reproductive structures called gemmae. These are particularly noticeable in the thalloid liverworts, such



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Figure 4. Near vertical rock face covered with mosses.



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Figure 5. Moss colonizing barren ground.



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Figure 6. Moss stabilizing a stream margin provides a seed bed for higher plant establishment.



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Figure 7. Fungus: *Galerina paludosa* growing specifically in *Sphagnum*.



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Figure 8. Fungus: *Spathularia flavida* growing in the moss *Hylocomium*.



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Figure 9. Fungus: *Cystoderma amianthinum* growing in a dense carpet of the moss *Hylocomium*.

as *Marchantia latifolia* (Figure 19), where one can often see fertile plants with their conspicuous umbrella-like structures, which bear the tiny spores, as well as gemmae cups with their disc-shaped gemmae within (Figure 20). In leafy liverworts, such as *Lophozia*, the gemmae are usually tiny, often light green or brown, and borne on the leaf margins (Figure 21). Mosses may also have gemmae on their leaves (Figure 22) and stems. Bryophytes are also capable of producing new plants by fragmentation of the shoots or even from parts of a leaf.

Habitats

Bryophytes play major roles in all of the diverse habitats found in Alaska, from the extensive wetlands of the North Slope through open shrub heathlands, black spruce dominated forests and wetlands, into white spruce, birch and aspen dominated boreal forests and temperate wetlands, and in alpine zones. In boreal forests and sub-Arctic heaths, lichens are also abundant and provide an important winter source of food for larger browsing animals, particularly caribou and, to a lesser extent, moose and musk ox (Figure 23).

The **alpine tundra** zones throughout Alaska are home to a number of specialist mosses adapted to the extreme cold-dominated and variably changing climates. *Andreaea* (Figure 24), *Grimmia*, *Racomitrium* and *Hedwigia* (Figure 25) species are commonly seen on rocks, and *Encalypta*, *Syntrichia*, *Bryum* (Figure 26) and others, such as *Oncophorus* (Figure 27), on soil.



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Figure 10. Dense insulating moss layer in a black spruce forest.

Figure 11. *Ptilium crista-castrensis*, an upland forest understory moss.

Figure 12. *Plagiomnium cuspidatum*, a moist habitat moss.

In sub-arctic heathlands mosses often form thick carpets that, over time, may develop thick peat layers that act

as huge carbon sinks. Increased global temperatures are likely to have a major impact on the decomposition rates of these

peat deposits with the potential release of huge amounts of the greenhouse gas carbon dioxide. Many bryophytes and lichens are found in these heathlands.

Much of Alaska's surface topography is classified as **wetland**, a term often misunderstood, misinterpreted, and a never-ending source of argument and litigation for construction and development industries. Mosses are now being used to further delineate the classification of wetlands. *Sphagnum* species (Figures 28, 29, 30, 31, 32) are very important components of the wetland bryoflora. Because of their unique structure, the plants can absorb vast quantities of moisture, a feature that led to *Sphagnum* being used in wound dressings, early sanitary pads, diapers, and now extensively in horticulture and in oil spill remediation. Their physiology gives these plants a unique ion exchange capacity and the ability to acidify their habitat, which excludes many other plants.

In **black spruce forests** a wide range of bryophytes, particularly *Hylocomium* (Figure 33), *Pleurozium* (Figure 34), *Dicranum* (Figure 35) and *Aulacomnium*, and lichens, such as *Peltigera*, *Cladina*, and *Cladonia*, form the dominant ground cover and may, over time, develop a significant duff layer that provides shelter for small mammals, a host of small invertebrates, as well as forming a deep insulating blanket over the ground below. Duff, like that from a spruce, is very easily burnt, with severe fires burning through to the mineral soil below.

In **boreal forests**, leaf litter may limit the occurrence of bryophytes and lichens,

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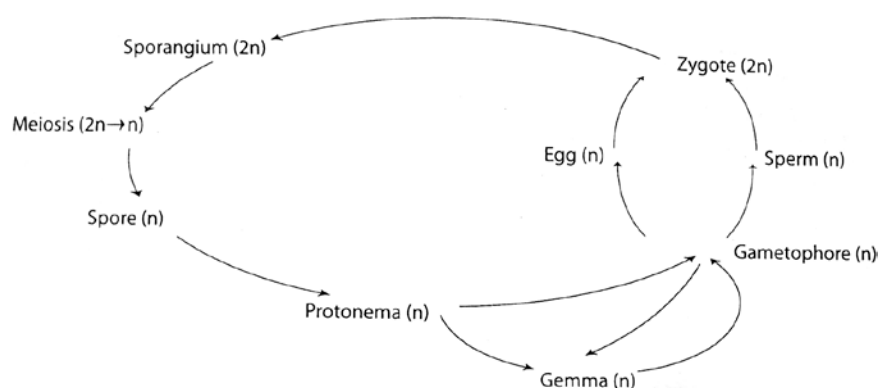


Diagram by Rodney D. Seppelt

Figure 13. Diagrammatic life history of bryophytes.

but extensive carpets of mosses such as *Hylocomium*, *Pleurozium*, *Dicranum*, and *Tomentypnum* (Figure 36), can be found along with a number of *Sphagnum* species.

Epiphytes. Mosses are not restricted to ground level substrates. Species such as *Orthotrichum* (Figure 37) occur on the trunks and smaller branches of many trees. *Pylaisiella* and some *Hypnum* species commonly form a skirt around the base of aspen trees (Figure 38). The liverwort *Ptilidium* (Figure 39) is often found closely adhering to the lower furrowed bark of aspen and on fallen logs. In moist temperate forests and in tropical regions, tree trunks and branches may be completely covered with a host of epiphyte species having a considerable influence on ecosystem water balance and nutrient cycling.

Bryophytes as Habitats for Other Organisms

Moisture is critical for survival and maintenance of bryophyte growth. Dense mats or clumps of mosses also retain

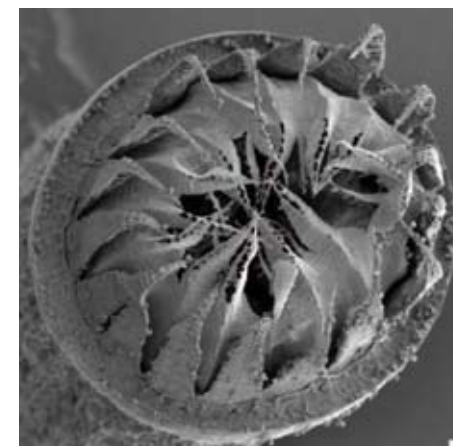
considerable amounts of moisture and increase the humidity of the many microhabitats within the moss mats. This is important for the survival of small animals that inhabit both the moss and the forest duff layer. The physiological activity of the moss, tiny animals and microbes that live within the moss clumps can elevate the carbon dioxide levels in the clumps to around 2,200 parts per million (ppm)—currently atmospheric levels are at about 390 ppm. A thick moss insulating layer may also protect and allow subsurface permafrost to come very close to the ground surface, thereby limiting non-cold hardy plants.

Because of their high phenolic compound content, mosses are generally not eaten by other animals. However, compounds such as arachidonic acid, a polyunsaturated fatty acid, may be present in high amounts in some mosses that are eaten in large amounts by some animals, such as reindeer, Soay sheep, barnacle geese, and may impart greater pro-



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Figure 14. *Polytrichum juniperinum* with capsules.

Figure 15. Scanning electron micrograph of double peristome of *Bryum*.

Figure 16. The liverwort *Riccia cavernosa*.

Figure 17. Moss: *Splachnum luteum* on old bear dung.

tection against the cold (Prins 1981). Birds and slugs may consume, and some actively search for, the almost ripe capsules of mosses. Most birds, small mammals and

even the larger browsing animals, generally avoid eating mosses. However, just prior to hibernation, bears may consume large amounts of moss, apparently to aid

binding of their digestive system and blocking defecation during their winter sleep.

Birds and small mammals often use mosses as nest material. Small ground-dwelling mammals (voles, shrews, and mice) burrow into and through deep layers of moss to reach relative safety from predators and to gain insulation from cold winter temperatures.

Large suites of fungi live on or in intimate association with mosses. Most high latitude species of *Galerina*, *Cystoderma*, *Arrhenia*, many species of *Mycena*, *Cudonia*, *Spathularia*, and some species of *Dentinum*, *Geoglossum*, *Microglossum*, *Cantharellula* and, on rare occasions, even some *Cortinarius* species, utilize mosses as substrates (Figures 40, 41, 42).

Mosses as Miniature Forests

There are many useful and fascinating features of leaves, such as the number of rows (2, 3, 4, 5 or more), shape and size, cell shape and size and surface ornamentation, cross-sectional anatomy, where and how the plant grows (on tree bark, rocks, soil, in water or bogs; flat and creeping on the substrate, or erect and often in tufts or large patches) that help identify these plants. It is features of the mature sporophyte that are most often needed, however, to confirm their identity.

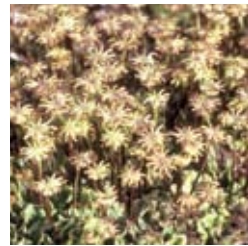
Because of the perceived difficulty in identifying bryophytes, along with the lichens and fungi, they are usually omitted from ecological surveys and, all too often, flora surveys. They are generally small in



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Figure 18. The dung inhabiting mosses, *Tetraplodon angustatus* (foreground) and *Tetraplodon mnioides* (background).

Figure 19. *Marchantia latifolia* with umbrella-like sporangiophore. Capsules are borne under the finger-like rays.

Figure 20. *Marchantia gemma* cups with gemmae.

Figure 21. Leafy liverwort, *Lophozia incisa*, with light green gemmae on leaf margins.

Figure 22. Moss *Syntrichia papillosa*, clusters of gemmae on inner leaf surfaces.

Figure 23. Musk ox feeding on moss.

Figure 24. Moss: *Andreaea rupestris*, grows on rock.

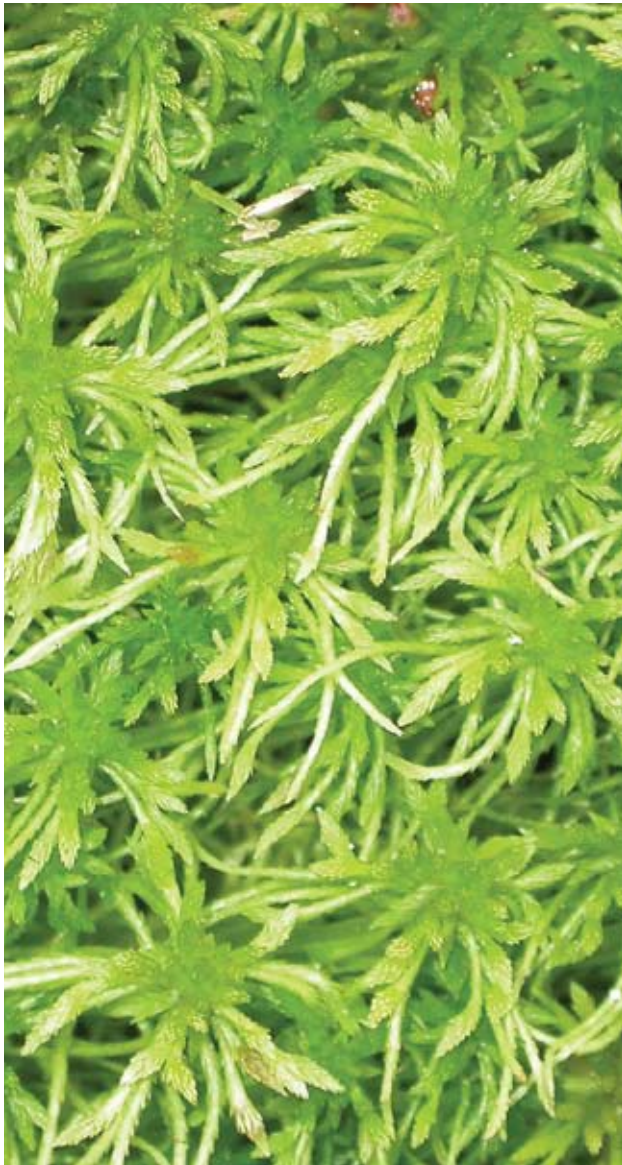
Figure 25. Moss *Hedwigia ciliata*, grows over rock and soil.

Figure 26. Moss *Bryum argenteum*, early colonist of bare ground.

Figure 27. Moss: *Oncophorus wahlenbergii*, a colonist of bare ground and disturbed areas.

Figure 28. *Sphagnum russowii*.

Figure 29. *Sphagnum angustifolium*.



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Figure 30. *Sphagnum girgensohnii*.



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Figure 31. *Sphagnum warnstorffii*.



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Figure 32. *Sphagnum squarrosum* with capsules.



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Figure 33. The stair-step feather moss: *Hylocomium splendens*, an abundant forest floor species.



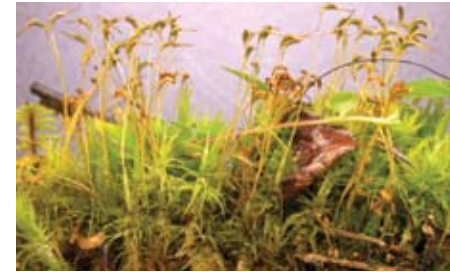
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Figure 34. Red-stemmed feather moss: *Pleurozium schreberi*, an abundant forest floor species.

size, but often in the habitats where they live, are the equivalent of the forests of more temperate climates.

What we recognize as a forest contains trees, shrubs, ground cover plants, birds, herbivore and carnivore vertebrate animals, small mammals and other small

animals, and below ground plant parts and a host of small or microscopic animals. So, too, a deep carpet or tuft of mosses can be viewed as a forest, although the scale of size is much smaller (Figures 43, 44). Small burrowing mammals and frogs, insects and their larvae, spiders and other



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Figure 35. The moss, *Dicranum polysetum*, with 2 or more mature sporophytes on each stem.



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Figure 36. The yellow-brown shiny shoots of the moss, *Tomentypnum nitens*, common in moist heath, shrub and woodland are unmistakable.



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Figure 37. *Orthotrichum speciosum*, a common moss on tree trunks, particularly aspen and cottonwood.



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Figure 38. Skirt of the mosses *Pylaisiella polyantha* and *Hypnum* at the base of aspen.

invertebrates, microscopic organisms such as fungi and bacteria, abound in the moss layer. A moss tuft or a carpet of moss is indeed the equivalent of a tall tree forest—but in miniature beneath your feet.

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Figure 39. The liverwort *Ptilidium ciliare* is common on fallen decaying wood and loosely attached. The browner *Ptilidium pulcherrimum* is tightly attached to bark or old wood. Both have small overlapping leaves with hairy margins.

Figure 40. Fungus: *Cystoderma fallax* grows on moss.

Figure 41. Fungus: *Cantharellula umbonata* grows on moss.

Figure 42. Fungus: *Cudonia circinans* grows on moss.

Figure 43. Dense mats of *Brachythecium* species are found on the ground, fallen leaf litter and rotting wood.

Figure 44. Tuft of *Grimmia pulvinata* on rock. Leaves have long white hair points.

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